

ON THE GEOGRAPHICAL DISTRIBUTION,  
ECOLOGY AND DISTINCTIVE FEATURES  
OF *LISTERA* × *VELTMANII* CASE

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Until recently the Veltman's hybrid Twayblade (*Listera* × *veltmanii* Case) was known only from the vicinity of the type locality in Alger Co., Michigan (Case 1964a, 1964b). Since both of its putative parents, *L. convallarioides* (Sw.) Nutt. and *L. auriculata* Wieg., grow in close proximity in other parts of the northeast, it seemed likely that the hybrid would occur elsewhere. This prediction was realized on 20 July, 1975, when we discovered *Listera* × *veltmanii* along the sandy banks of the Pancake River near the Lake Superior shore, Algoma Dist., Ontario. A subsequent search of some major northeastern herbaria (AMES, CAN, DAO, GH, LKHD, NEBC, TRT) revealed that the hybrid, although rare, is widely distributed in northeastern North America (fig. 1). Whenever collected it was confused with either one or the other of its putative parents. Since the ten new and widely separated stations now known, in addition to the type locality, represent the total known distribution of this hybrid, the specimen data are fully cited below.

**CANADA:** **New Brunswick:** KENT CO.: mountain back of Claire, 17 July 1904, A. A. Eaton (AMES 2567). **Newfoundland:** GRAND FALLS DIST.: low alluvial woods, north bank of river below the falls, Grand Falls, valley of Exploits River, 10 July 1911, M. L. Fernald and K. M. Wiegand 5242 (AMES 84315). ST. GEORGE DIST.: Harry's Brook, Black Duck, 27 June 1930, Rachel B. Kennedy (AMES 84265). BONA-VISTA SOUTH DIST.: Terra Nova National Park, 14 July 1962, R. D. Muir (DAO). **Quebec:** GASPE WEST CO.: alluvial wooded banks, Riviere St. Anne des Monts, 3-17 August 1905, 16 July 1906, M. L. Fernald and J. F. Collins (AMES 84271, CAN 16751 & 16748). CHARLEVOIX CO.: Ste.-Anne-des-Lacs, Lac Barn, 11 July 1968, G. Lemieux 14256 (DAO). **Ontario:** ALGOMA DIST.: cedar swamp near Duck Harbour, vicinity of Michipicoten Harbour, 29 July 1938, R. C. Hosie et al. (CAN 16732); cedar swamp at Rahal Lake, vicinity of Michipicoten Harbour, 15 July 1938, R. C. Hosie et al. (TRT 55174); in coarse sandy soil along the spring-flooded banks of river under alders, Pancake River near Lake Superior shore, 20 July 1975, P. M.



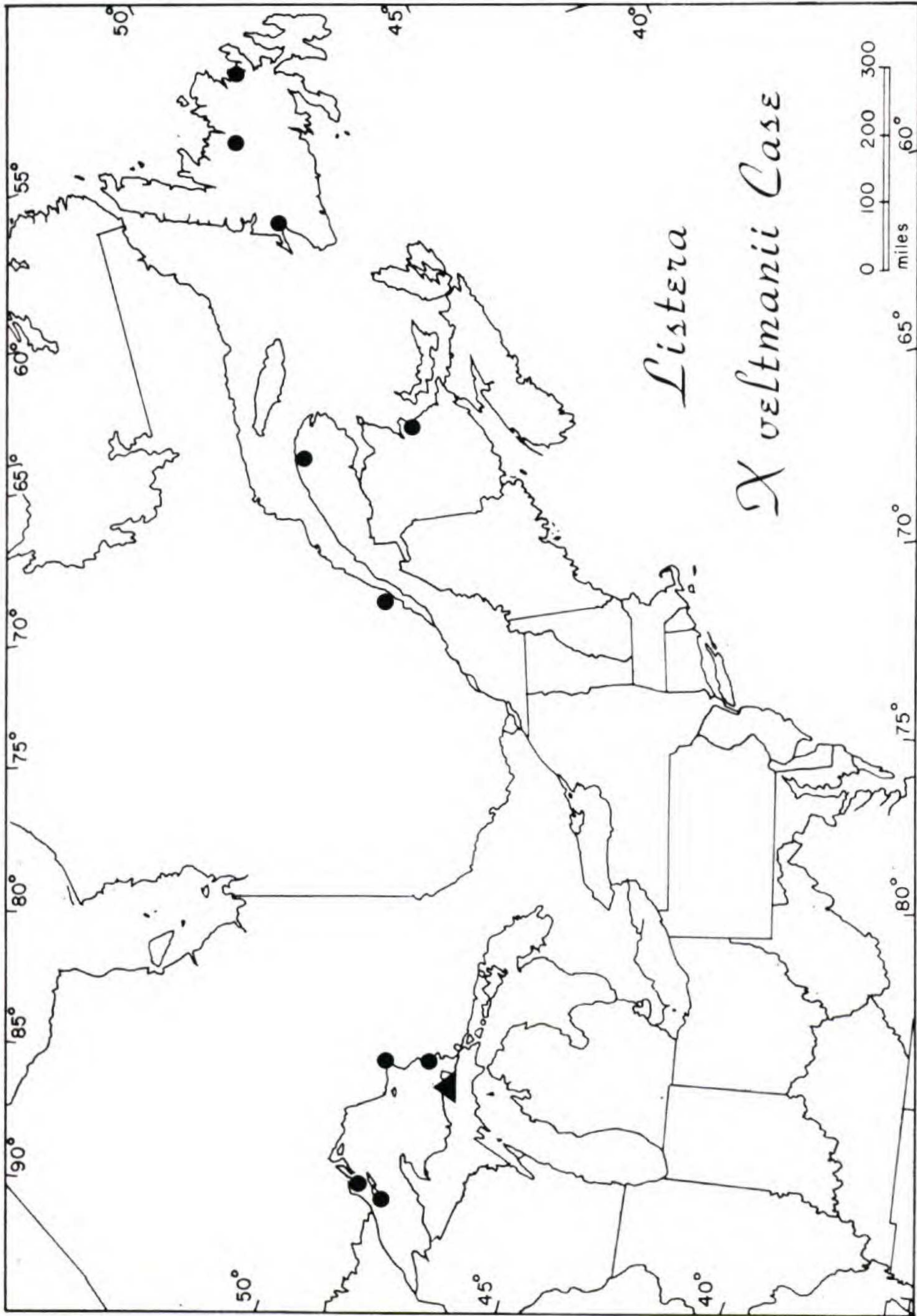


Fig 1. Distribution of *L. X veltmanii* Case based on specimens at AMES, CAN, DAO, GH, LKHD, NEBC and TRT. The general area surrounding the type locality is indicated with a solid triangle.



Catling, K. L. McIntosh, and S. M. McKay (TRT 181960, 181961, DAO, CAN). THUNDER BAY DIST.: moist boggy soil under cedars, northwest corner of Perry's Bay, Silver Islet, Sibley Penn., 22 July 1950, C. E. Garton et al. (AMES 84868, DAO, LKHD 3660, TRT 78051); same as preceding, 6 August 1972, C. E. Garton 15163 (LKHD 30858). UNITED STATES: Michigan: ISLE ROYALE: mixed open woods, Grace Harbour, 7 July 1930, C. A. Brown 3220 (CAN 200860).

Although Case (pers. comm.) reports finding large colonies of intermediate plants at Grand Marais, Michigan, which were clearly not  $F_1$  hybrids, only two sheets were found in the herbaria searched that may have represented backcrosses (with *Listera convallarioides*). On one of these the apparent backcross plants were mounted with some more typical hybrids from Duck Harbour, Ontario (cited above). The other sheet represented a collection from Summit Depot, New Brunswick (on calcareous peat under cedar and tamarack by Loon Lake, Mad. Co., 22 July 1960, G. C. Cunningham and O. L. Loucks, s.n. (DAO)).

In a few cases the hybrids were found on the same sheet with typical specimens of one of the parents: the specimen of *Listera*  $\times$  *veltmanii* from Claire, New Brunswick, as well as that from Rahal Lake, Ontario, were mounted on the same sheet with *L. convallarioides*, and hybrids from Harry's Brook, Newfoundland, were mixed with typical *L. auriculata*. In almost all cases one or both putative parents have been collected from the same location as the hybrid. Case (*loc. cit.*) has also reported finding the hybrid in association with either one or the other parent.

At Pancake Bay an ecological separation between the hybrids and the putative parents was apparent. *Listera auriculata* was quite frequent (ca. 100 flowering plants in  $\frac{1}{4}$  mile) on the moist sandy banks of the Pancake River under alders (*Alnus rugosa* (DuRoi) Spreng.) with the primary associates being the mosses *Atrichum oerstedianum* (C. Mull.) Mitt. and *Hypnum lindbergii* Mitt., and the liverwort, *Pellia epiphylla* (L.) Corda. Other frequent associates included *Carex intumescens* Rudge, *Equisetum sylvaticum* L., *Rubus pubescens* Raf., *Viola* cf. *nephrophylla*



Greene, *Onoclea sensibilis* L., *Pyrola minor* L., *Scutellaria lateriflora* L., *Aster lateriflorus* (L.) Britt., and *Streptopus amplexifolius* (L.) DC. var. *denticulatus* Fassett. This is a characteristic habitat and association for *L. auriculata* in Ontario.

*Listera convallarioides* was not found in the immediate area of the seasonally flooded riverbanks, but about 20-40 metres up some of the intermittent streams in a forest of White Birch (*Betula papyrifera* Marsh). Here it was growing profusely (at least 200 flowering plants) among the sedges in the black mucky soil of a streambed. The sedge community was dominated by *Carex scabrata* Schwein. Other associates included *Carex stipata* Muhl., *Carex intumescens* Rudge, *Eupatorium maculatum* L., *Circaea alpina* L., *Viola* cf. *nephrophylla* Greene, *Aster lateriflorus* (L.) Britt., *Aster umbellatus* Mill., *Veronica americana* (Raf.) Schw., and several bryophytes (*Mnium* spp., etc.).

About thirty flowering plants of *Listera* × *veltmanii* were found along the sandy river banks near plants of *L. auriculata*. At least twenty grew in an apparently more unstable habitat where much sand covered the ground (fig. 2a), and only *Atrichum oerstedianum*, *Equisetum sylvaticum* and *Carex intumescens* were frequent associates. These habitats sometimes occurred where streams drained into the river from the surrounding forests. Generally the hybrids were found in small, widely scattered groups of one to five plants, and only in a few cases were they in very close association (within a few metres) with *L. auriculata*. To some extent a distinct and perhaps intermediate type of habitat was characteristic of the hybrid, and the hybrid habitat was certainly more disturbed. Case (1964b, p. 71) similarly noted that *L.* × *veltmanii* grew in a habitat "that was not exactly typical of that of either parent", and he also noted "considerable evidence of physical disturbance."

At Pancake Bay all of the plants of *Listera* found could easily be assigned to either *L.* × *veltmanii*, *L. auriculata*,



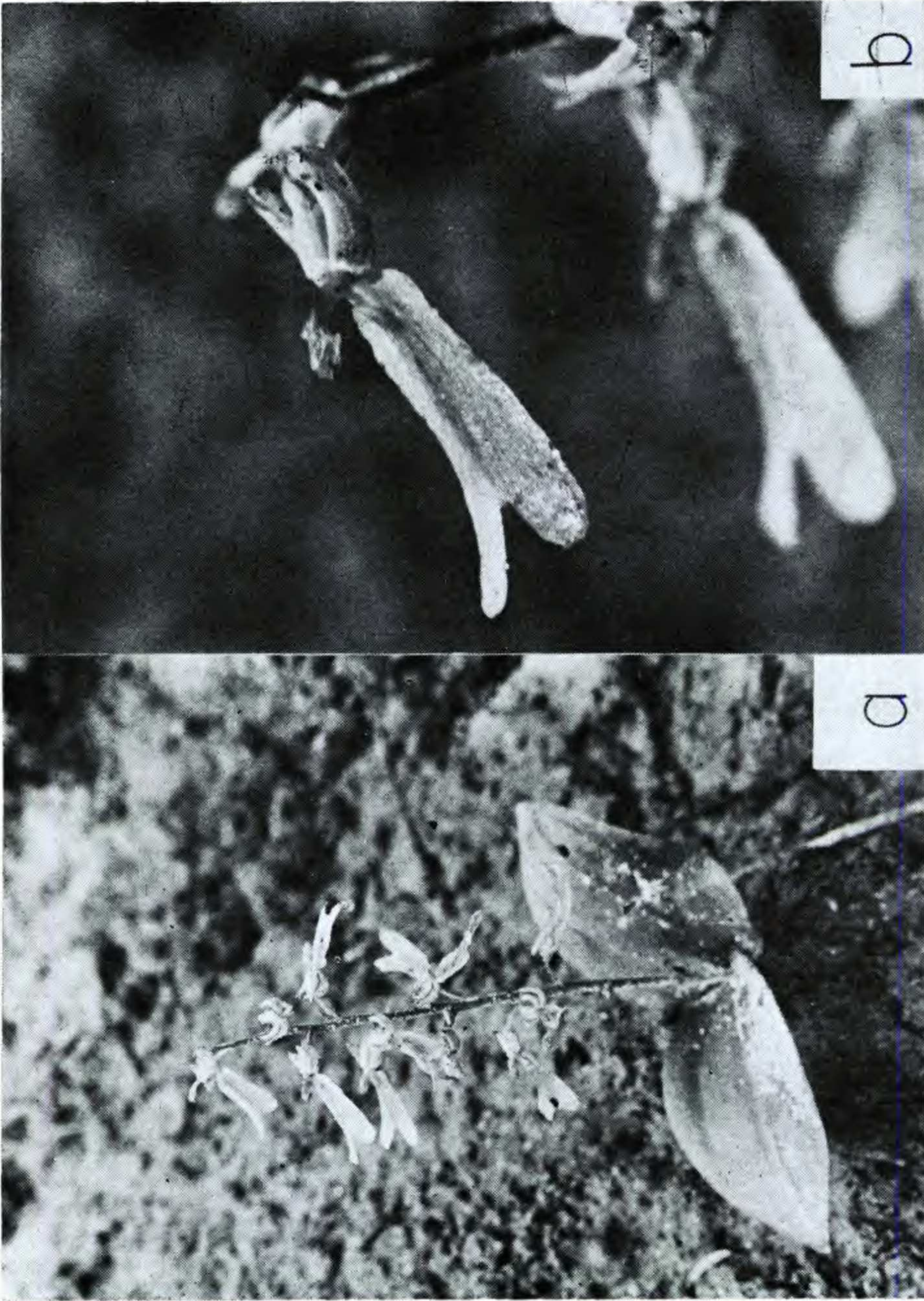


Fig. 2. *Listera*  $\times$  *veltmanni* Case photographed near the mouth of the Pancake River, Algoma Dist., Ontario. a, plant growing in coarse sand near riverbank. b, close-up of flower showing short claw and partial auricle at base of lip.



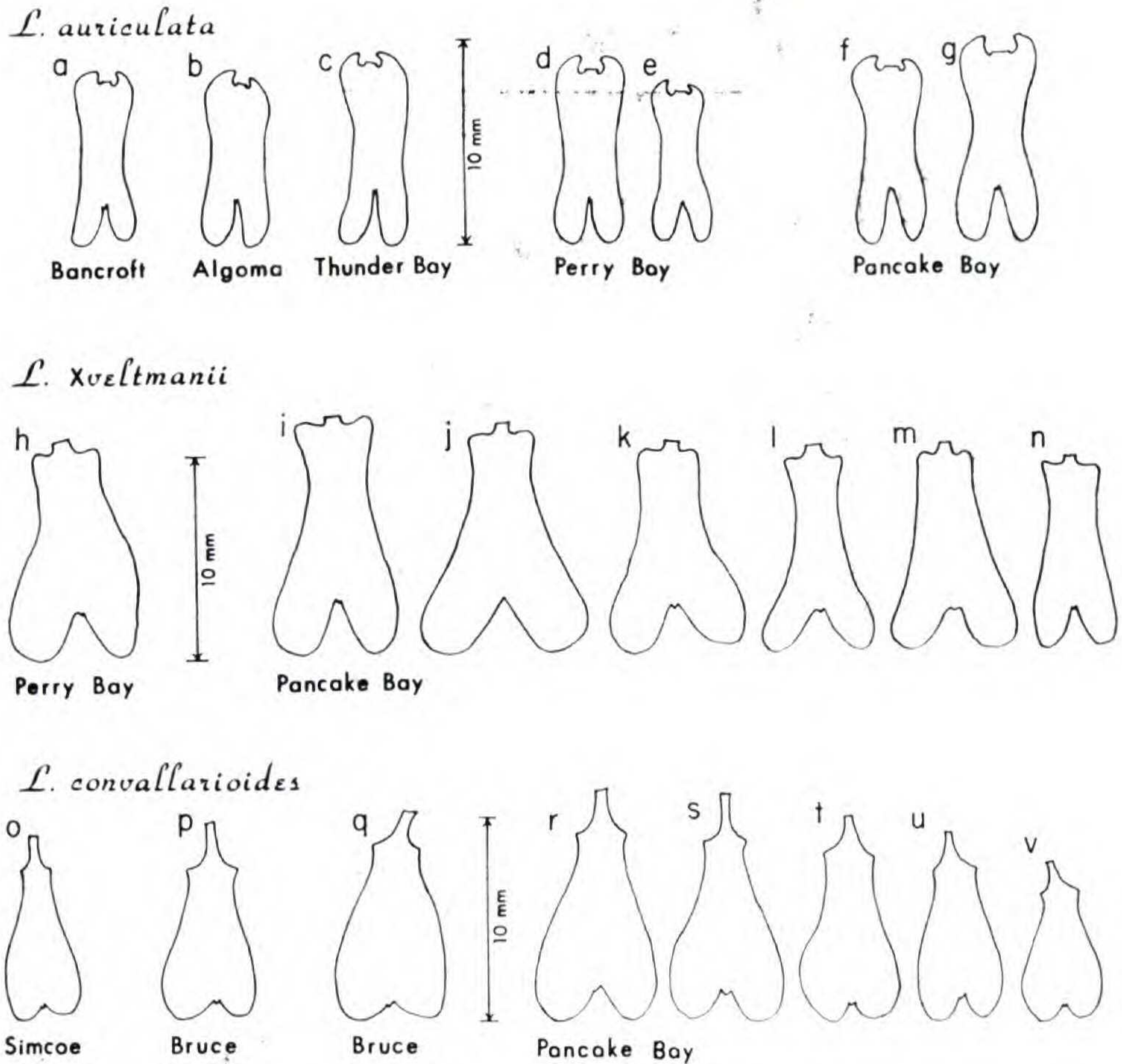


Fig. 3. Camera lucida drawings of the lips of *Listera* spp.

a-g, *Listera auriculata*. a, York R., near Bancroft, Hastings Co., 45°04', 77°44' (TRT 181742). b, Michipicoten Harbour, Algoma Dist., 48°00', 85°00' (TRT 55177). c, Jackfish Lake, 48°45', 87°15', Thunder Bay Dist. (TRT 49731). d, e, Perry Bay, Thunder Bay Dist., 48°20', 88°50' (TRT 181952). f, g, Pancake Bay, Algoma Dist., 46°57', 84°41' (TRT 181957).

h-n, *L. xveltmanii*. h, Perry Bay, Sibley Peninsula, Thunder Bay Dist. (TRT 78051). i-n, Pancake Bay, Algoma Dist. (TRT 181960, 181961).

o-v, *L. convallarioides*. o, Bass Lake, Simcoe Co., 44°35', 79°31' (TRT 148120). p, Lymburner Lake, Bruce Co., 45°11', 81°20' (TRT 161002). q, Cape Croker, Bruce Co., 44°56', 81°01' (TRT 38541). r-v, Pancake Bay, Algoma Dist. (TRT 181955).



or *L. convallarioides*. The extremes in variation of lip shape were collected, and are illustrated in figure 3. When these were compared with lip outlines from other stations it became clear that both putative parents and hybrids were quite typical. For instance, *Listera auriculata* from Pancake Bay, and from Perry Bay (where the hybrid has also been found), was quite similar to *L. auriculata* from locations where *L. convallarioides* and the hybrid are unknown (fig. 3a-3c). Similarly *L. convallarioides* from Pancake Bay was comparable with *L. convallarioides* throughout its range including Bruce and Grey Counties, Ontario, where *L. auriculata* and *L. × veltmanii* are not known to occur (fig. 3o-3q). This would seem to further establish the rarity of backcrossing.

The lip of *Listera × veltmanii* is quite distinctive in having a relatively short claw and in being very slightly auricled at the base (fig. 2b, 3h-3n). *L. auriculata* is almost without a claw and has well developed auricles, while *L. convallarioides* is long-clawed with basal prominences ("teeth"). In addition the lips of *L. × veltmanii* and *L. convallarioides* tend to be distally widened (cuneate) whereas *L. auriculata* is often as wide basally as distally, or slightly widened only in the distal third. In *L. × veltmanii* the lip tends to have more convex lateral margins while in *L. convallarioides* the lateral margins are concave for at least the distal third of their length. Finally the apical sinus is over 1/5 of the length of the lip in *L. × veltmanii* and *L. auriculata*, but usually much less in *L. convallarioides*. It is important to note that some variation in lip shape, especially the apical dilation, is correlated with position of the flower in the raceme. Flowers nearer to the top of the raceme tend to have lips that are less apically dilated than those below. Figures 3m and 3n illustrate this well, since both were taken from the same raceme, fig. 3n representing the terminal (14th) flower while fig. 3m represents the third flower from the base.

Other floral parts have not been quantitatively studied, but intermediacy is apparent in some cases. For instance,



the width of the lateral petals and length of the column of *Listera* × *veltmanii* tend to be intermediate between the putative parents. In length of the floral parts the hybrids are generally closer to *L. convallarioides*. At maturity the ovaries of *L. × veltmanii* are similar to *L. convallarioides* in being more ascending and less anteriorly gibbous than *L. auriculata*.

As well as in these floral characters *Listera* × *veltmanii* frequently differs from its putative parents in being much larger (up to 2.5 dm.). Also, in *L. × veltmanii* the glandular pubescence of the flower pedicels is generally shorter and more sparse than that of the main axis. In *L. convallarioides* this glandular pubescence is just as thick and long on the pedicels as on the main axis of the raceme, and extends in a somewhat reduced form over the ribs of the ovary. In *L. auriculata* the flower pedicels and ovary are glabrous.

A final interesting distinction concerns flowering time. When we visited the Pancake River on 20 July we found several plants of *Listera* × *veltmanii* in full anthesis, and many plants still had several upper flowers intact, but all plants of *L. auriculata* and *L. convallarioides* were either past anthesis with all of the flowers quite withered, or with only a few of the uppermost flowers intact. Judging from the dates accompanying some herbarium specimens, it would seem that *L. × veltmanii* continues flowering somewhat later than its putative parents at other stations as well.

The fact that *Listera* × *veltmanii* is presently known only where the ranges of the putative parents overlap further suggests that Case was correct in assuming the plant to be a hybrid. *Listera auriculata* has a northeastern distribution extending from the Lake Superior region north to Hudson Bay and east to northern New England and the Canadian Maritime Provinces. In the east *L. convallarioides* overlaps with *L. auriculata*, but extends further to the south in New England and in the Great Lakes region. Unlike *L. auriculata* it ranges west across southern Canada



to the Pacific coast and southward in the mountains. In parts of the east where *L. convallarioides* extends further south than *L. auriculata*, no *L. × veltmanii* has been found despite the relatively more intensive floristic study of these areas. The absence of *L. × veltmanii* outside the region of sympatry of the putative parents therefore seems real.

Although this interesting hybrid is rare, it has likely been overlooked in some areas. Its apparent restriction to the sympatric distribution of the parents, its widespread occurrence, and frequent association with the putative parents, would seem to suggest spontaneous hybridization and low hybrid fertility. The fact that *Listera × veltmanii* is frequently quite distinct, and that the putative parents nearby are also quite distinct, suggests that the hybrid is often somehow effectively isolated from its parents.

#### ACKNOWLEDGEMENTS

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